

Exploitation of differential temperature-sensitivities of crops for improved resilience of tropical smallholder cropping systems to climate change: A case study with temperature responses of tomato and chilli

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ABSTRACT

Increasing air temperatures due to long-term global climate change are predicted to exert substantial negative impacts on a majority of agricultural crops in the tropics, where most smallholder farms have a mixture of crops. Modification of the composition of cropping systems by incorporating crop species with greater growth and yield performance at higher temperatures is an important adaptation option. Accordingly, the principal objective of the present work was to demonstrate the feasibility of utilizing the differential temperature sensitivities of tropical crops to increase resilience of smallholder farming systems in the tropics to climate change, taking tomato and chilli in a case study. Tomato (cv. *Thilina*) and chilli (cv. *MI-Green*) crops were grown with adequate water, nutrients and recommended crop protection in a multi-locational field experiment traversing an altitudinal gradient (15–1200 m), which represented a gradient in seasonal mean temperature (T_a) ranging from 18.7 to 30 °C, over four consecutive seasons (Dec. 2012–Oct. 2014) in the humid- and sub-humid zones of Sri Lanka. Temperature response functions were estimated by linear regression of growth and yield parameters against T_a . Across the tested range of T_a , fruit yield of tomato showed a significant negative linear trend with increasing T_a (@ 2.83 Mg ha⁻¹ °C⁻¹) while the pod yield of chilli showed a significant positive linear trend (@ 0.51 Mg ha⁻¹ °C⁻¹). While the total biomass accumulation followed the same trend as fruit/pod yield, the harvest index of both crops showed significant negative trends, thus indicating the sensitivity of reproductive processes to increasing temperature. In tomato, fruit yield was significantly positively correlated to individual fruit weight, which decreased significantly with increasing temperature. In contrast, in chilli, pod yield was significantly positively correlated to number of pods per plant, which increased significantly with increasing temperature. These findings demonstrate the possibility of increasing the resilience of annual cropping systems in the tropical zone to future climate change by modifying their species composition via replacement of crops that are sensitive to higher temperatures (e.g. tomato) with those that are tolerant (e.g. chilli). The corresponding response functions to seasonal temperature extremes showed that biomass production, its partitioning to yield and yield of both crops were more sensitive to increases in seasonal mean daytime maximum temperature than to increases in night-time minimum temperature. However, yield responses to the diurnal temperature difference showed that differential sensitivity of the two crops to night-time minimum temperatures also played a significant role in determining their yield responses. These findings are useful in designing future cropping systems with greater resilience to climate change.

1. Introduction

There is strong evidence that air temperatures have shown a significant increasing trend during the last century (Hartmann et al.,

2013), at both global and regional scales. They have also increased in terms of daily and seasonal means as well as daily and seasonal maxima and minima (Donat and Alexander, 2012). Furthermore, the frequency of high temperature extremes has increased while that of cold extremes

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has decreased during the last few decades (Alexander et al., 2006; Lobell et al., 2011). As temperature is a key determinant of growth and developmental processes of crops increased air temperatures will have a substantial impact on crop yields (Lobell and Field, 2007; Lobell et al., 2011; Porter et al., 2014). While positive impacts of increasing temperatures have been reported for some high-latitude regions (Supit et al., 2010), the large majority of studies has reported negative impacts on crop yields in the tropical zone (Lobell et al., 2008; Knox et al., 2012; Porter et al., 2014 and references therein; Rosenzweig et al., 2014). There is strong evidence that temperatures exceeding 30–34 °C, depending on the crop species and region, have clear negative impacts on key yield-determining physiological processes and yields (Porter et al., 2014). In particular, high temperature episodes and their increased frequency during the critical reproductive phase of crops could cause substantial yield losses (Battisti and Naylor, 2009; Welch et al., 2010; Hatfield et al., 2011; Gourdji et al., 2013). There is evidence that future temperature increases could have negative impacts on crop yields even in the currently cooler, higher latitudes (Porter et al., 2014). In the tropical zone, even slight warming in the range of 1–2 °C could decrease yields in the absence of adaptations (Porter et al., 2014). In particular, region-wise meta-analyses of climate impacts have identified South Asia and Southern Africa as regions of high vulnerability to climate change in the near-term up to 2030 (Lobell et al., 2008), with Knox et al. (2012) predicting an average yield decline of 8% across all crop species by 2050. These adverse impacts of future increases in temperature on the yields of major crop species will exert a significant strain on global, regional and local food security, especially given the estimated increasing demand of 14% per decade (Alexandros and Bruinsma, 2012). In addition to the projected yield decline, inter-annual variability of crop yields have been projected to increase with future climate change (Porter et al., 2014), thus increasing instability in food supply and reducing food security (Wheeler and von Braun, 2013).

Minimizing adverse impacts of climate change in general and of increasing temperatures in particular will require various adaptations in the cropping systems and their management practices (Howden et al., 2007). In a meta-analysis of yield responses to a range of agronomic crop management adaptations, an average yield gain of 15–18% has been estimated across a local average warming ranging from 1 to 5 °C (Porter et al., 2014). A key adaptation option, which would be applicable for almost all crops and regions across the world, is the development of heat tolerant crop cultivars through conventional and molecular plant breeding (Gourdji et al., 2013; Porter et al., 2014). However, this is a slow process requiring several years to decades so that alternative adaptation options have to be explored. One such option would be to use the inherent variability among different crop species in their temperature thresholds (Hatfield et al., 2011) and temperature responses to modify the existing cropping systems and sequences to stabilize their productivity in a future warmer climate. Here, the aim is to ensure that crop species that are most adapted and suited to the prevailing temperature regimes are grown. This could result in significant shifts in the cultivation area of a given crop (Porter et al., 2014) or changes in the composition of crops grown in a given region. There is already evidence of farmer adaptation to climate change by changing crop species and cultivars and modifying sowing dates (Bryan et al., 2009; Porter et al., 2014 and references therein), with an average yield advantage of 17% in comparison to the current practices. Notably, the above adaptations have resulted in greater yield gains than other agronomic adaptations such as optimization of irrigation and fertilizer management. Therefore, we hypothesize that in view of the broader range of crops grown in the tropics, especially in smallholder farms, effective adaptation to climate change is possible through changes in the crop composition in the existing cropping systems in the near-future until new cultivars of greater heat tolerance become available. Accordingly, the principal objective of this work is to demonstrate the feasibility of utilizing the differential temperature sensitivities of tropical crops to increase resilience of smallholder

farming systems in the tropics to climate change. As a case study, two Solanaceous vegetable crops of global importance, tomato (*Lycopersicon esculentum* Mill.) and chilli (*Capsicum annum* L.), have been used.

2. Materials and methods

2.1. Experimental locations and cropping seasons

A multi-locational field experiment was conducted in the sub-humid zone of Sri Lanka during four consecutive seasons from November 2012 to October 2014 (Supplementary Tables S1 and S2). The experimental locations traversed an altitudinal gradient (i.e. from 15 to 1200 m above mean sea level), and therefore a temperature gradient, which enabled determination of temperature response functions of crops grown. Specific locations were the Agricultural Research Station, Rahangala (RG), the Experimental Farm of the University of Peradeniya, Kundasale (KD), the Field Crops Research and Development Institute, Mahailuppallama (MI) and the Regional Agricultural Research and Development Center, Kilinochchi (KN). These locations represented different agro-ecological regions of Sri Lanka (Punyawardaane, 2008). Essential climatic and soil parameters of the locations are summarized in Supplementary Table S3.

Cropping seasons, as defined by the respective dates of transplanting and final harvesting, overlapped in three out of the four locations, with Rahangala (RG) being the exception. In seasons 1 and 3, which are locally known as the *maha* season, transplanting was done with the onset of North-East Monsoon rainy season in December and final harvesting in late March to early April. In seasons 2 and 4 (*yala* season), transplanting was done in May with the final harvesting in September to October. In comparison to the other three locations, cropping seasons were longer at RG because of its lower temperatures. This meant that as the four seasons progressed sequentially, both transplanting and final harvesting at RG lagged behind those of other locations.

2.2. Crop establishment and maintenance

Widely grown cultivars of tomato (cv. *Thilina*) and chilli (cv. *MI-green*) were sown in nurseries. Tomato seedlings were transplanted three weeks after sowing and chilli after four weeks on the 5 m × 5 m experimental plots as separate sole crops (Supplementary Tables S1 and S2). However, the tomato crops established at Kilinochchi (KN) in Seasons 2 and 4 and at RG in Season 4 were destroyed by severe drought. Although the chilli crops grown at Mahailuppallama (MI) and KN in Season 1 were affected by excessive rainfall, they were not destroyed. Inter-row and intra-row spacings of 80 cm × 50 cm and 60 cm × 45 cm were used for tomato and chilli, respectively. In tomato, one seedling was transplanted per hill whereas in chilli two seedlings were transplanted per hill. All crop management practices, including fertilizer application, for the two crops were done as recommended by the Department of Agriculture, Sri Lanka (Anonymous, 1992). Details of fertilizer application are given in Supplementary Table S4. Weed control was done manually. Pests and diseases were controlled by periodic spraying of recommended chemicals. Specifically, limited incidence of late blight, caused by *Phytophthora infestans*, was observed in tomato crops at all locations. This was controlled chemical sprays of *Metalaxyl*. Crops were maintained without experiencing soil water deficits by periodic irrigations during rain-free periods. Tomato fruits were harvested at 80% red colour in several picks while chill pods were also harvested in several picks once they became dark green (Supplementary Tables S1 and S2).

2.3. Experimental design and measurements

The experimental treatments were the two crops (tomato and chilli) grown across the four locations during four seasons in a Randomized

Complete Block Design with three blocks at each location. Daily meteorological data were recorded using automated weather stations (Watchdog, 2900ET) located at the experimental locations. Numbers of days from transplanting to 50% flowering, to the first harvest and to maturity (i.e. final harvest) were counted. A destructive sampling of four randomly selected plants per plot were taken to measure the leaf area index at 50% flowering ($LAI_{50\%}$), total biomass at 50% flowering ($TBM_{50\%}$) and total biomass at final harvest (TBM_{fh}). Measurements were limited to four plants because of the high uniformity of plant stands within each plot. Ten plants were selected from the middle of the plot to measure tomato fruit yield and chilli pod yield and yield components. As fruits of tomato and pods of chilli initiated and matured continuously during the post-flowering period, several fruit and pod harvests were made from the same sets of 10 plants. Final yield was calculated as the sum of all fruit and pod harvests and are presented in terms of both fresh and dry weights. The fresh-dry weight ratio for tomato fruits and chilli pods was measured in a series of representative sub-samples at each harvest to compute an average ratio for each crop. The same sub-samples of fruits/pods were used to measure the mean individual fruit/pod weights. Harvest index (HI) was calculated as the ratio between total fruit/pod dry weight and TBM_{fh} . $LAI_{50\%}$ was measured using an automatic leaf area meter (AAM9, Hayashi Denko Co. Ltd, Tokyo). Dry weights of leaves, stems, roots and fruits/pods were measured by oven drying at 60 °C to a constant weight. Crop growth rate up to 50% flowering ($CGR_{50\%}$) and post-flowering crop growth rate ($CGR_{p\%}$) were calculated as the dry weight gains per unit land area per day during the respective periods.

2.4. Data analysis

The count data were subjected to non-parametric analysis (PROC CATMOD) while parametric data were analyzed using the General Linear Model (PROC GLM) procedure in Statistical Analysis System (SAS), Version 9.0. To quantify the response of tomato and chilli to changing environmental temperature across locations and seasons, analyses were carried out separately for the two crops. When locations and seasons were required to be compared, locations and seasons were considered as the treatment factors. The four seasons were treated as independent environments and were considered to be nested within locations and the location effect was tested using ‘seasons (location)’ as the error term. Mean separation was done using confidence intervals calculated from the respective standard errors of mean and degrees of freedom. All mean comparisons are presented at $P < 0.05$ unless stated otherwise.

Inter-relationships among growth parameters (i.e. $LAI_{50\%}$, $TBM_{50\%}$ and TBM_{fh}), fruit/pod yield and yield components were determined by linear correlation analysis. The response of growth and yield parameters of each crop to the temperature gradient represented by different locations and seasons were quantified by fitting linear or second-order polynomial functions against the mean location temperature during each season using regression analysis. The best fitted relationship was obtained based on the highest coefficient of determination (R^2). Parallel regressions were carried out using seasonal mean night-time minimum (T_{min}) and daytime maximum (T_{max}) temperatures as the independent variable to determine their respective influences on different parameters of crop growth and yield. Respective contributions from the variation of different climatic factors towards the observed yield variation of the two crops were estimated by multiple linear regression analysis using the Forward Selection Procedure in SAS Version 9.0. Initially, regressions were run with seasonal means of daily mean temperature (T_a), relative humidity, daily irradiance (I_d) and seasonal total incident radiation (I_{Tot}) as independent variables. Subsequently, regressions were run after replacing T_a with seasonal means of T_{max} and T_{min} in order to determine the respective contributions from the variation of diurnal temperature extremes.

The respective cumulative thermal times required for key

phenological events (i.e. 50% flowering and final harvest of fruits/pods at maturity) were calculated using the cardinal temperatures (i.e. base, optimum and ceiling temperatures) that were estimated based on the fitted relationship between the rate of progress to final harvest at different locations and the respective daily mean temperatures during the period from transplanting to final harvest (T_a). The rate of progress to final harvest was calculated as the reciprocal of the duration from transplanting to final harvest (t). In both crops, second-order polynomial functions were fitted to $(1/t)$ against T_a . Base (T_b) and ceiling temperatures (T_{ce}) were estimated as the polynomial function's intercepts on the temperature axis while the optimum temperature (T_{opt}) was estimated as the T_a at maximum $(1/t)$.

Cumulative thermal time for a given phenological event, i.e. the thermal duration (θ), was calculated as,

$$\theta = \sum_{i=1}^t (T_a - T_b) \quad (1)$$

For the days on which T_a exceeded T_{opt} , an effective temperature (T_e) was calculated from the fitted polynomial function as the temperature on the sub-optimal range having the same $(1/t)$ as that at the respective supra-optimal T_a . In both crops, the calculated T_e replaced T_a in Eq. (1) for the days on which T_a exceeded T_{opt} .

3. Results

3.1. Variation of meteorological conditions at different experimental locations during the four cropping seasons

Seasonal total rainfall (RF_{tot}) (Supplementary Table S5) and its within-season distribution (Supplementary Fig. S1) showed substantial variation among the four seasons in all four locations. At RG, RF_{tot} exceeded 400 mm in all seasons except Season 3 (S3). In all other locations, RF_{tot} was less than 400 mm in all seasons except Season 1 (S1) and S3 at KD. Rainfall was well-distributed throughout the season in S1 at all locations and in S2 at RG and KD. In other seasons and locations, there were appreciable rain free periods, notably in S3 at all locations and in S4 at MI and KN. Even though S4 at RG received a very high RF_{tot} (1189 mm), the rain free period at its beginning destroyed the tomato crop due to severe drought. It is notable that ca. 20% of total seasonal rainfall at KN in S1 was received during a single day of extremely high rainfall (226 mm).

In all seasons, RG experienced substantially lower daily mean temperatures (T_a) than the other three locations (Fig. 1a). Among these locations, temperatures of KN and MI were higher than those at KD, with the difference being greater in S2 and S4, which are the two *yala* seasons. These differences were reflected in the respective seasonal means of T_a as well (Supplementary Tables S6 and S7). In *yala* (S2 and S4), T_a s at KN were consistently higher than those at MI whereas in *maha* (S1 and S3) such a consistent difference could not be seen. As a result, while seasonal mean T_a of KN was greater than that of MI by 1.2 °C in *yala*, the corresponding difference was lower (-0.2–0.9 °C) in *maha*. At the three warmer locations (i.e. KD, MI and KN) where the cropping seasons overlapped, T_a showed an increasing trend within the two *maha* seasons whereas no such trend was observed in *yala* (Fig. 1a). At RG, where the seasons were longer, an increasing trend of T_a was observed only in S3. The night-time minimum (T_{min}) and the daily maximum (T_{max}) temperatures showed broadly similar patterns of variation (Fig. 1b and 1c) to the corresponding pattern of T_a . However, there were some notable exceptions as well. For example, in contrast to the pattern shown by seasonal means of T_a and T_{min} , the seasonal mean T_{max} of KN was greater than that of MI only in one (S2) out of the four seasons (Supplementary Table S7). Furthermore, in S3, all three warmer locations had similar mean seasonal T_{max} . Notably, T_{min} and T_{max} showed greater within-season fluctuation than T_a and this was reflected in their greater standard errors (Supplementary Tables S6 and

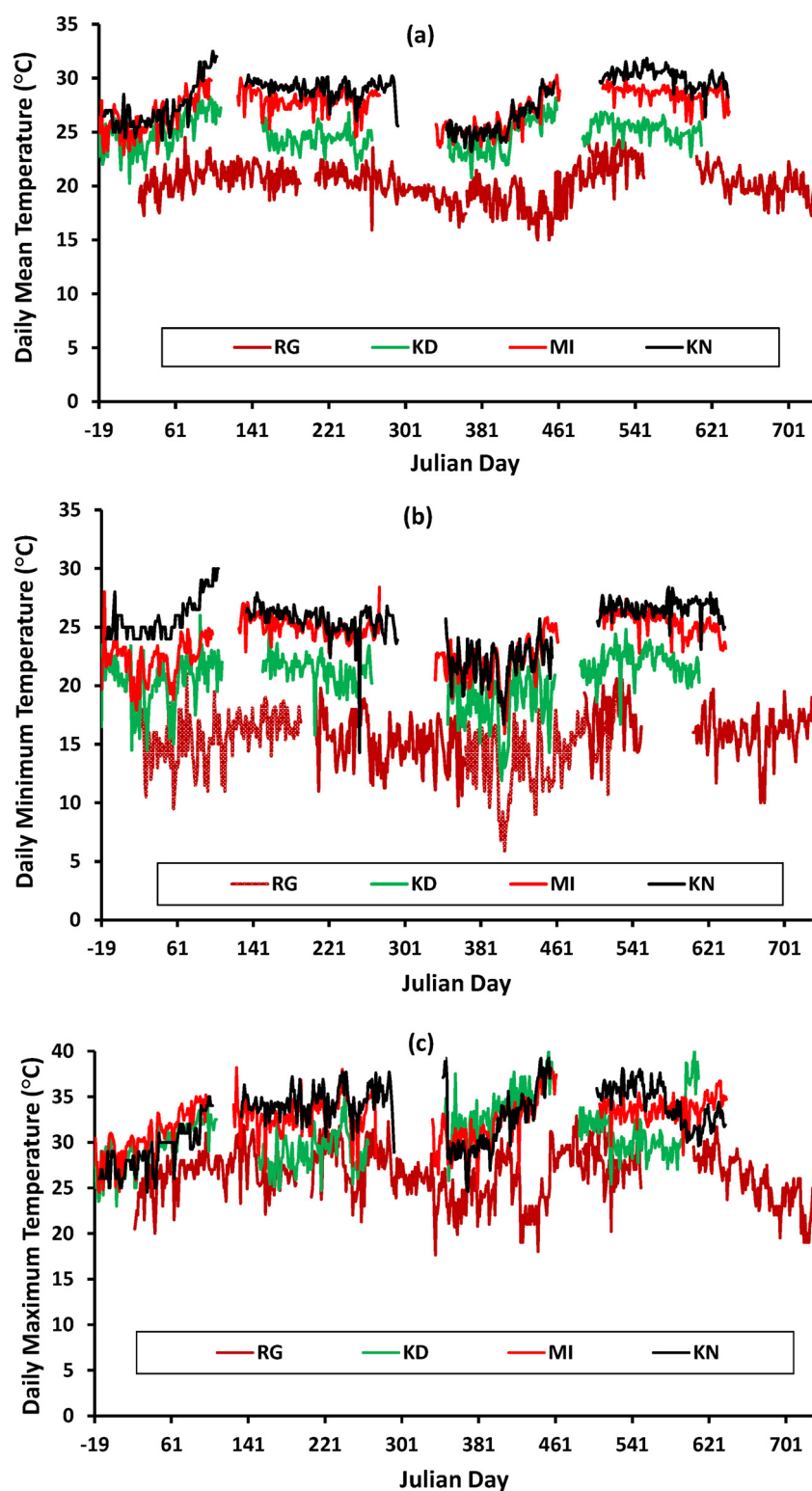


Fig. 1. Seasonal variation of (a) daily mean (T_a), (b) minimum (T_{min}) and (c) maximum (T_{max}) air temperatures at different locations during the four cropping seasons for tomato and chilli. Note the difference in Y-axis scales.

S7). In terms of seasonal means of T_a , T_{min} and T_{max} , the *yala* seasons were warmer than the *maha* seasons at MI and KN whereas no such differences were evident at RG and KD.

The diurnal temperature difference, D_{Temp} (i.e. the difference between the seasonal means of maximum day-time temperature and minimum night-time temperature) ranged from 3.2 to 15.3 °C across different locations and seasons and showed a decreasing trend with

decreasing altitude (Supplementary Table S8). Accordingly, the two high- and mid-elevation locations (RG and KD) showed greater D_{Temp} than the two low-elevation locations (MI and KN) in a majority of seasons.

There was no significant variation in mean seasonal relative humidity (RH) during the *maha* season (i.e. Seasons 1 and 3) across different locations (Supplementary Table S9). However, during the *yala*

Table 1

Days to 50% flowering and final harvest and the respective thermal durations of tomato grown at different locations and cropping seasons.

Site	Days to 50% flowering				Thermal duration to 50% flowering (°C d)				Days to final harvest				Thermal duration to final harvest (°C d)			
	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4
RG [*]	47	47	50	60	381	413	363	645	114	101	113	*	1126	897	789	*
KD	42	33	32	31	447	359	354	297	109	98	96	100	1138	1049	1016	943
MI	36	37	33	27	362	229	345	171	109	119	109	130	991	893	1080	893
KN	42	50	38	35	397	303	401	178	93	*	102	*	841	*	915	*

^{*}RG-Rahangala; KD-Kundasale; MI-Mahailluppallama; KN-Kilinochchi; S1-S4-Seasons 1–4; *Crop destroyed by severe drought. Different replicates did not show variation in the days to 50% flowering and final harvest.

season (Seasons 2 and 4), mean seasonal RH in the two warmer sites (MI and KN) was 7–14% lower than in the two cooler sites (RG and KD).

The seasonal average daily irradiance (I_d) showed appreciable variation among locations and seasons (Supplementary Table S10) primarily because of the variation in cloudiness. However, there were no consistent variation patterns. Even though I_d was higher at the two warmer locations (i.e. MI and KN) during Season 1, this pattern was not shown consistently in the three seasons that followed. The total solar radiation incident upon the crops over the entire season (I_{Tot}) varied considerably across locations and seasons because of the variation of total crop duration (Tables 1 and 2), which was a function of the temperature variation experienced by them, and the daily irradiance.

Despite the variation in total crop durations across the locations, I_{Tot} was strongly, positively correlated ($r > 0.90$, $P < 0.0001$) with I_d . However, none of these two measures of solar irradiance showed significant correlations with the seasonal means of daily mean temperature or daily relative humidity across the different locations and seasons. The seasonal means of daily mean temperature and daily RH experienced by tomato were not significantly correlated. However, the corresponding seasonal means experienced by chilli, were significantly, negatively correlated ($r = -0.63$, $P = 0.0082$).

3.2. Estimated cardinal temperatures

The fitted second-order polynomial functions enabled T_b , T_{opt} and T_{ce} of tomato to be estimated as 11.8, 23.6 and 35.4 °C, respectively (Supplementary Fig. S2.a). The corresponding cardinal temperatures of chilli, estimated similarly, were 13.9, 24.6 and 35.4 °C (Supplementary Fig. S2.b).

3.3. Variation of crop phenology across locations and cropping seasons

In both crops, different replicate plots at a given location did not show variation in the days to 50% flowering (N_{50f}) and days to final harvest (N_{fh}). However, there was appreciable variation in both parameters among locations within a given season and among seasons within a given location (Tables 1 and 2). With a few exceptions, N_{50f} and N_{fh} were greatest at the coldest site RG. In general, the number of days decreased with increasing location temperature. The notable exceptions were: the longer N_{50f} in tomato at KN in Season 2 and in chilli

at MI in Season 1; the longer N_{fh} in tomato at MI in Seasons 2 and 4 and in chilli at MI and KN in Season 2. The cumulative thermal times (i.e. thermal durations) for the two phenological events also varied among locations and seasons for both crops (Tables 1 and 2). When averaged across the 16 different environments (i.e. four locations $\times$ four seasons), the respective thermal durations from transplanting to 50% flowering (θ_{50f}) were 353 ± 28 and 379 ± 31 °C days for tomato and chilli, respectively. The corresponding mean thermal durations from transplanting to final harvest (θ_{fh}) were 967 ± 28 and 955 ± 46 °C days.

3.4. Variation of growth and yield parameters at different locations and seasons

The effect of seasons, which was considered to be nested within locations, was highly significant ($P < 0.0001$) on all measured growth and yield parameters of tomato (Table 3). In chilli also, the season (location) effect was highly significant on all parameters except total biomass at final harvest (TBM_{fh}). On the other hand, in tomato the location effect was significant ($P < 0.05$) only on fresh and dry fruit yields (Y_f and Y_d) and crop growth rate up to 50% flowering (CGR_{50f}). In contrast, in chilli the location effect was significant on the majority of parameters with the number of pods per plant (NPP), individual pod fresh weight (IPFW) and harvest index (HI) being the exceptions.

3.5. Correlations between growth and yield parameters

In tomato, fresh fruit yields (Y_f) showed a highly significant ($P < 0.0001$) positive correlation ($r = 0.888$, $n = 39$) with their corresponding fruit yields expressed on a dry weight basis (Y_d). Similarly, in chilli also, Y_f and Y_d were strongly, positively correlated ($r = 0.810$, $n = 48$, $P < 0.0001$). As commercial yields of both tomato and chilli are expressed on a fresh weight basis, the respective Y_f data have been used in examining correlations between growth and yield parameters.

In tomato, Y_f showed significant positive correlations with LAI_{50f} , TBM_{fh} , CGR_{pfl} and HI (Table 4). Out of the two yield components, only IFFW showed a significant positive correlation with Y_f . Notably, there was a significant negative correlation between Y_f and CGR_{50f} . Among the growth parameters, LAI_{50f} showed significant positive correlations with TBM_{50f} and TBM_{fh} while TBM_{50f} had significant positive

Table 2

Days to 50% flowering and final harvest and the respective thermal durations of chilli grown at different locations and cropping seasons.

Site	Days to 50% flowering				Thermal duration to 50% flowering (°C d)				Days to final harvest				Thermal duration to final harvest (°C d)			
	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4
RG [*]	83	82	75	53	571	512	368	371	154	133	116	125	1086	761	682	798
KD	41	36	44	41	391	399	409	344	104	97	107	124	1108	1156	992	1226
MI	64	40	40	36	613	289	402	228	114	139	121	128	981	1039	1095	877
KN	46	39	38	33	430	211	383	149	115	159	112	99	913	1003	1030	528

^{*}RG-Rahangala; KD-Kundasale; MI-Mahailluppallama; KN-Kilinochchi; S1-S4-Seasons 1–4; Different replicates did not show variation in the days to 50% flowering and final harvest.

Table 3Significance (*P*) of the season and site effects for growth and yield parameters of tomato and chilli grown at different locations and cropping seasons.

Effect	LAI _{50fl}	TBM _{50fl}	TBM _{fh}	CGR _{50fl}	CGR _{pf}	NFP (NPP)	IFFW (IPFW)	Y _f	Y _d	HI
<i>Tomato</i>										
Season (Location)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Location	ns	ns	ns	0.0004	ns	ns	ns	0.0242	0.0554	ns
<i>Chilli</i>										
Season (Location)	< 0.0001	0.0002	ns	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Location	0.0075	< 0.0001	< 0.0001	< 0.0001	0.0019	ns	ns	0.0118	0.0015	ns

Season (Location)–Seasons considered as nested within locations; ns–Non-significant at *P* = 0.05.LAI_{50fl}–Leaf area index at 50% flowering; TBM_{50fl}–Total biomass at 50% flowering; TBM_{fh}–Total biomass at final harvest; CGR_{50fl}–Crop growth rate from transplanting to 50% flowering; CGR_{pf}–Crop growth rate from 50% flowering to final harvest; NFP–Number of tomato fruits per plant; NPP–Number of chilli pods per plant; Y_f and Y_d– Fruit yield of tomato or Pod yield of chilli in terms of fresh and dry weights respectively; HI–Harvest index.

correlations with CGR_{50fl} and TBM_{fh}. TBM_{fh} and CGR_{pf} were significantly positively correlated. IFFW had significant negative correlations with CGR_{50fl}, TBM_{50fl} and TBM_{fh}. HI also had significant negative correlations with TBM_{50fl} and CGR_{50fl} while having a significant positive correlation with IFFW.

In chilli, Y_f had highly-significant positive correlations with all growth parameters (i.e. LAI_{50fl}, TBM_{50fl}, TBM_{fh}, CGR_{50fl}, CGR_{pf}) and NPP (Table 5). All growth parameters were also highly significantly positively correlated to each other. Out of the two yield components, NPP had significant positive correlations with all growth parameters except CGR_{pf}. On the other hand, HI showed significant negative correlations with all growth parameters.

3.6. Response of growth and yield parameters to increasing temperature

In tomato, LAI_{50fl}, Y_f, Y_d and HI showed significant (*P* < 0.05) negative linear reductions with increasing mean location temperature (T_a) (Fig. 2 and Supplementary Fig. S3). Tomato fruit yield, given as a fresh weight, decreased with increasing T_a at the rate of 2.83 Mg ha^{−1} for each 1 °C increase in T_a. The corresponding rates of reduction for Y_d and HI were 91.14 kg ha^{−1} °C^{−1} and 0.03 per °C. Among the rest of the parameters, TBM_{50fl}, TBM_{fh} and IFFW also showed decreasing trends with increasing T_a which did not achieve statistical significance because of the presence of 1 – 2 outliers (Supplementary Fig. S3). The regressions became significant (*P* < 0.05) when the outliers were not considered. In contrast, NFP did not show any trend with T_a.

In chilli, LAI_{50fl}, TBM_{50fl}, TBM_{fh}, NPP, Y_f and Y_d showed significant (*P* < 0.05) positive linear relationships with T_a (Fig. 2 and Supplementary Fig. S4). Chilli pod yield, measured as a fresh weight, increased

by 0.52 Mg ha^{−1} per °C rise in T_a while dry chilli yield increased at the rate of 49.43 kg ha^{−1} °C^{−1}. In contrast, HI showed a significant negative linear relationship with T_a, with the rate of reduction being 0.03 per °C (Supplementary Fig. S4). IPFW, which did not show a significant trend initially, also showed a significant negative linear relationship with T_a when three outliers were excluded.

In tomato, Y_f and HI showed significant (*P* < 0.05) negative linear relationships with both mean seasonal minimum (T_{min}) and maximum (T_{max}) temperatures (Fig. 3 and Supplementary Fig. S5). The respective regression slopes were greater for T_{max} than T_{min}, indicating greater sensitivity of Y_f and HI to T_{max}. In contrast, TBM_{fh} did not show significant relationships with either T_{min} or T_{max}. However, significant (*P* < 0.05) negative relationships were shown when 1–2 outliers were not considered. Here again, TBM_{fh} showed substantially greater sensitivity to increasing T_{max} than to increasing T_{min}.

In chilli, significant (*P* < 0.05) positive linear relationships were shown by Y_f and TBM_{fh} with both T_{min} and T_{max} (Fig. 3 and Supplementary Fig. S6). Final yield (Y_f) had a greater sensitivity to T_{max} (0.49 Mg ha^{−1} °C^{−1}) than T_{min} (0.44 Mg ha^{−1} °C^{−1}). In contrast, HI showed significant negative relationships with T_{min} and T_{max}, with the sensitivity being greater for T_{max} (−0.36 °C^{−1} as compared to −0.21 °C^{−1}).

In tomato, Y_f showed a significant (*P* < 0.05) positive relationship with the diurnal temperature difference (D_{Temp}) (Fig. 4). While Y_d also showed a similar trend, it was not statistically-significant. In contrast, Y_d of chilli had a significant negative relationship with increasing D_{Temp}, whereas the corresponding trend for Y_f of chilli was not significant. Fresh or dry yields of both crops did not show any significant linear or non-linear relationships with either seasonal total or daily incident solar radiation or relative humidity (data not shown).

Table 4

Linear correlation coefficients among growth and yield parameters of tomato grown in four locations during four cropping seasons.

	LAI _{50fl}	TBM _{50fl}	TBM _{fh}	CGR _{50fl}	CGR _{pf}	NFP	IFFW	HI
Y _f	0.570 ^a (0.0002) ^b	−0.046 ns	0.453 (0.0038)	−0.456 (0.0035)	0.453 (0.0038)	0.088 ns	0.500 (0.0012)	0.704 (< .0001)
LAI _{50fl}	–	0.588 (< .0001)	0.506 (0.001)	0.190 ns	0.217 ns	0.162 ns	0.011 ns	0.172 ns
TBM _{50fl}		–	0.372 (0.0199)	0.746 (< .0001)	−0.106 ns	0.229 ns	−0.468 (0.0027)	−0.335 (0.0371)
TBM _{fh}			–	0.135 ns	0.746 (< .0001)	0.099 ns	−0.331 (0.0396)	−0.065 ns
CGR _{50fl}				–	−0.028 ns	0.237 ns	−0.599 (< .0001)	−0.679 (< .0001)
CGR _{fh}					–	−0.166 ns	−0.013 ns	0.190 ns
NFP						–	0.118 ns	−0.067 ns
IFFW							–	0.653 (.001)

^a Pearson Linear Correlation Coefficient.^b Probability of the correlation coefficient being not significantly different from zero; Correlations among LAI_{50fl}, TBM_{50fl} and CGR_{50fl} had 45 observations while the rest had 39 observations; ns–Non-significant at *P* = 0.05.

Table 5

Linear correlation coefficients among growth and yield parameters of chilli grown in four locations during four cropping seasons.

	LAI _{50fl}	TBM _{50fl}	TBM _{fh}	CGR _{50fl}	CGR _{pf}	NPP	IPFW	HI
Y _f	0.439 ^a (0.0018) ^b	0.503 (0.0003)	0.703 (< .0001)	0.642 (< .0001)	0.423 (0.0027)	0.542 (< .0001)	−0.042 <i>ns</i>	0.132 <i>ns</i>
LAI _{50fl}	–	0.669 (< .0001)	0.667 (< .0001)	0.699 (< .0001)	0.418 (0.0031)	0.305 (0.0351)	0.109 <i>ns</i>	−0.351 (0.0144)
TBM _{50fl}		–	0.814 (< .0001)	0.964 (< .0001)	0.618 (< .0001)	0.366 (0.0105)	−0.116 <i>ns</i>	−0.409 (0.0039)
TBM _{fh}			–	0.838 (< .0001)	0.846 (< .0001)	0.294 (0.0427)	−0.196 <i>ns</i>	−0.400 (0.0049)
CGR _{50fl}				–	0.537 (< .0001)	0.465 (0.0009)	−0.087 <i>ns</i>	−0.372 (0.0092)
CGR _{pf}					–	0.021 <i>ns</i>	−0.293 (0.0432)	−0.336 (0.0195)
NPP						–	−0.024 <i>ns</i>	−0.057 <i>ns</i>
IPFW							–	0.163 <i>ns</i>

^a Pearson Linear Correlation Coefficient.^b Probability of the correlation coefficient being not significantly different from zero; All correlations had 48 data points; ns–Non-significant at $P = 0.05$.

Multiple regression analysis of both tomato and chilli yields against the respective seasonal environmental variables (i.e. seasonal mean temperature, season total incident irradiance, seasonal mean daily irradiance and seasonal mean relative humidity) showed that variation in seasonal mean temperature contributed most to the observed yield variation (Supplementary Table S11). When T_a was replaced with seasonal means of T_{min} and T_{max} , variation of T_{min} across locations and seasons explained most of the observed yield variation (Supplementary Table S12).

4. Discussion

4.1. Differential temperature responses of the two crops and their implications for adaptation of upland cropping systems to climate change

The present work clearly showed the existence of contrasting responses to increasing temperature among different crop species, with the yields of tomato showing a negative response while those of chilli showing a positive response within the range of temperatures experienced. These findings show the possibility of increasing the resilience of annual cropping systems to future climate change by modifying their species composition via replacement of crops that are sensitive to higher temperatures (e.g. tomato) with those that are tolerant (e.g. chilli). This can be part of farm diversification to increase climate resilience of small holder agricultural systems in the tropics (Porter et al., 2014).

It has to be acknowledged that successful crop replacement in a future warmer climate requires the fulfilment of a range of economic and sociological considerations in addition to having greater climate resilience. The climate-resilient crop (e.g. chilli) that would replace a climate-vulnerable crop (e.g. tomato) has to be economically profitable and the farmers should have the expertise and technology needed for its successful cultivation. Interchanging currently-grown crops with new crops with greater adaptability to changed climatic conditions could also entail appreciable changes in farming practices and farmer behaviour. As such, effective crop replacement could be a complex process. However, we argue that the smallholder farmers in the tropics, who usually cultivate a range of annual crops in their farms, are better placed to readily adopt crop replacement than large-scale farmers. They are highly sensitive to fluctuating prices and market demands for different crops and show a greater willingness to change the crops that they cultivate from season-to-season. Specifically, within the context of this study, both tomato and chilli have a high consumer preference and market demand. Therefore, replacement of tomato with chilli is not likely to affect the farmers economically.

The superior performance of tomato at the lower temperatures demonstrates its suitability in cropping systems at mid- and upper-elevations in the tropics. Therefore, the market demand for tomato could be fulfilled by expansion of tomato cultivation to relatively cooler regions of the tropics. Introduction of such zonation in crop cultivation could increase the overall climate resilience of crop production at the national scale in climate-vulnerable tropical countries such as Sri Lanka.

Use of heat-tolerant varieties in climate-vulnerable crops such as tomato is an alternative option to crop replacement. However, the few currently available heat tolerant tomato varieties in Sri Lanka are not popular among farmers because of their inferior fruit quality. Development of new crop varieties that combine heat tolerance with other desirable traits will require more time, especially in the developing countries of the tropical zone. Therefore, crop replacement will remain a viable practical option until suitable heat-tolerant varieties become available.

This study highlighted the temperature sensitivity of the crop reproductive processes (Jagadish et al., 2007) as the harvest index (HI) of both crops had responded negatively to increasing temperatures. This means that the scope for increasing the resilience of annual cropping systems to future warming via crop replacement will have an upper limit. Continuous warming will probably bring the yields of crops such as chilli also in to a negative phase once an upper threshold temperature is exceeded as the negative impacts on reproductive processes begin to outweigh the positive impacts on growth processes. It is notable that HI of both crops has shown higher temperature sensitivities to seasonal means of T_{max} than to those of T_{min} . This indicates that reproductive processes of both tomato and chilli will be more sensitive to future temperature extremes at the upper end.

The differential response to increasing temperature in the two crops tested here has come about primarily because of the difference in the influence of HI in yield determination in the respective crops. The strong positive correlation between HI and fresh fruit yield (Y_f) of tomato showed the strong influence of HI in determining the temperature response of tomato. This when coupled with the moderately strong positive correlation between total biomass at final harvest (TBM_{fh}) and Y_f meant that tomato yields declined with increasing temperature as both HI and TBM_{fh} showed significant negative temperature responses. In contrast, the absence of a significant correlation between HI and Y_f of chilli meant that HI did not have a controlling influence on the temperature response of chilli within the range of temperatures experienced by chilli crops of this experiment. The strong positive correlation between TBM_{fh} and Y_f of chilli coupled with the significant positive response of TBM_{fh} to increasing temperature meant that chilli yields

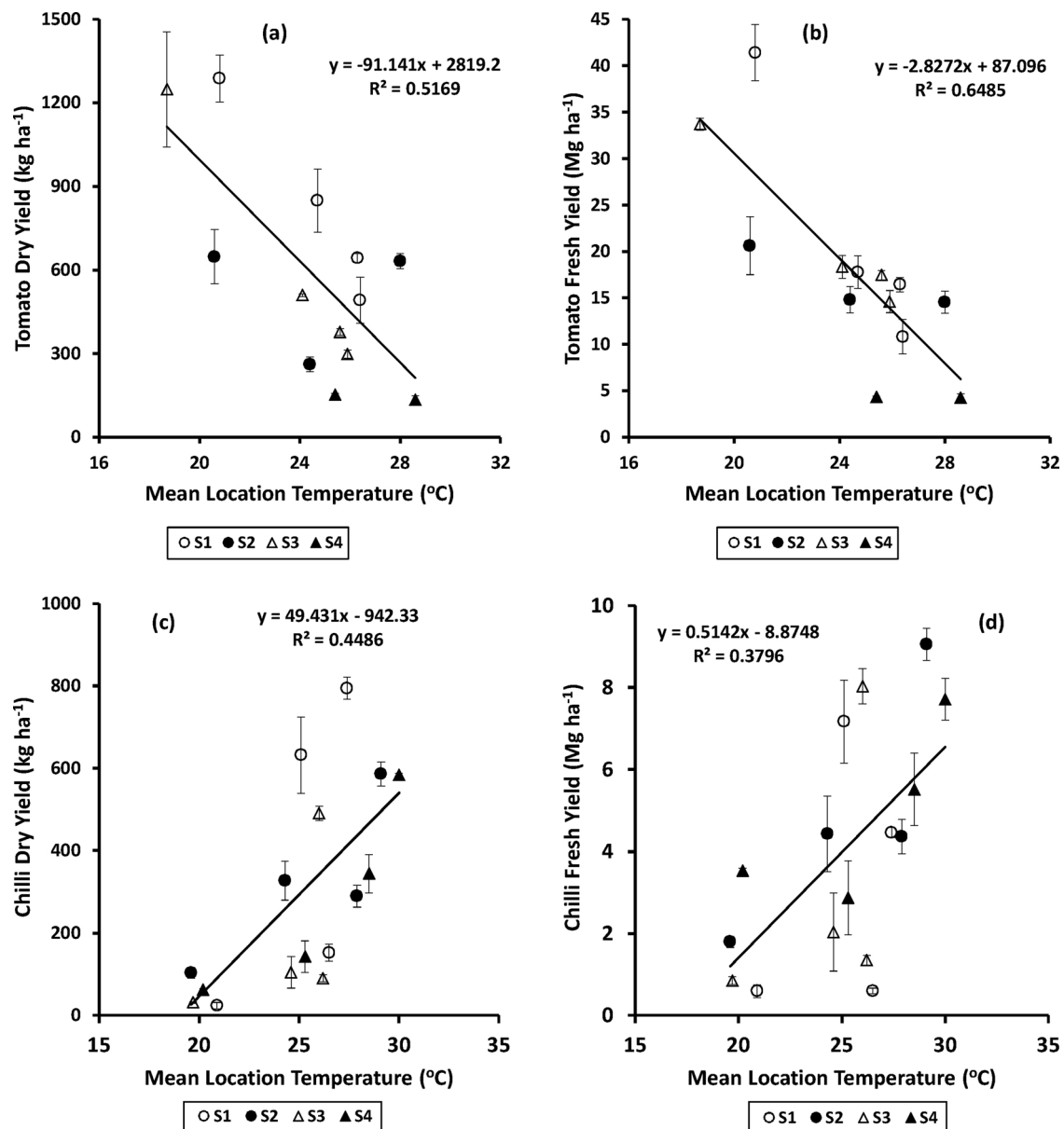


Fig. 2. Variation of dry and fresh yields of tomato and chilli with mean location air temperature: (a) Dry fruit yield of tomato (Y_d); (b) Fresh fruit yield of tomato (Y_f); (c) Dry pod yield of chilli; (d) Fresh pod yield of chilli. S1–S4 denote the four cropping seasons. Each data point is a mean of three replicate plots. Vertical error bars indicate the standard error of mean.

responded positively to increasing temperatures in spite of the significant negative response of HI to increasing temperatures.

It is notable that in addition to the greater sensitivity of HI of tomato to T_{max} , its TBM_{th} also showed a substantially higher sensitivity to increasing T_{max} than to T_{min} . This showed that in addition to reproductive processes, the physiological processes responsible for biomass accumulation (e.g. photosynthesis) in tomato also had greater sensitivity to increasing temperatures at the upper end. In contrast, the positive responses of TBM_{th} of chilli did not show an appreciable difference in its respective sensitivities to seasonal means of T_{max} and T_{min} , thus indicating the greater resilience of the growth processes of chilli to temperature fluctuations.

The contrasting relationships that the yields of these two crops had with the diurnal temperature difference (D_{Temp}) (Fig. 4) also provide important insights in to the underlying physiology in determining their yield responses to the co-variation of T_{max} and T_{min} . Increasing D_{Temp} increased the fresh fruit yields (Y_f) of tomato (Fig. 4a) primarily due to its greater tolerance of lower night-time temperatures (T_{min}), which was

the principal reason for increased D_{Temp} . Besides, lower T_{min} probably reduced the respiratory losses and contributed to increasing tomato yield. In contrast, greater sensitivity to lower T_{min} brought about the decrease in the dry pod yields of chilli with increasing D_{Temp} (Fig. 4d). Therefore, predicted increases in T_{min} with future climate change (Donat and Alexander, 2012) could contribute to decreasing tomato yields while increasing chilli yields in the future. Linear regressions showed that yields of both crops had a greater sensitivity to day-time maximum temperature (T_{max}) than night-time minimum temperatures (T_{min}) (Fig. 3). However, multiple linear regressions involving all climatic variables (i.e. seasonal total and daily mean irradiances and seasonal means of relative humidity) along with seasonal means of T_{max} and T_{min} in place of T_a showed that variation in T_{min} explained the highest proportion of yield variation of both crops (Supplementary Table S12). This underlined the importance of differential sensitivity of these two crops (and of tropical crops in general) to future variations in day- and night-time temperatures and their differential in determining their yield response.

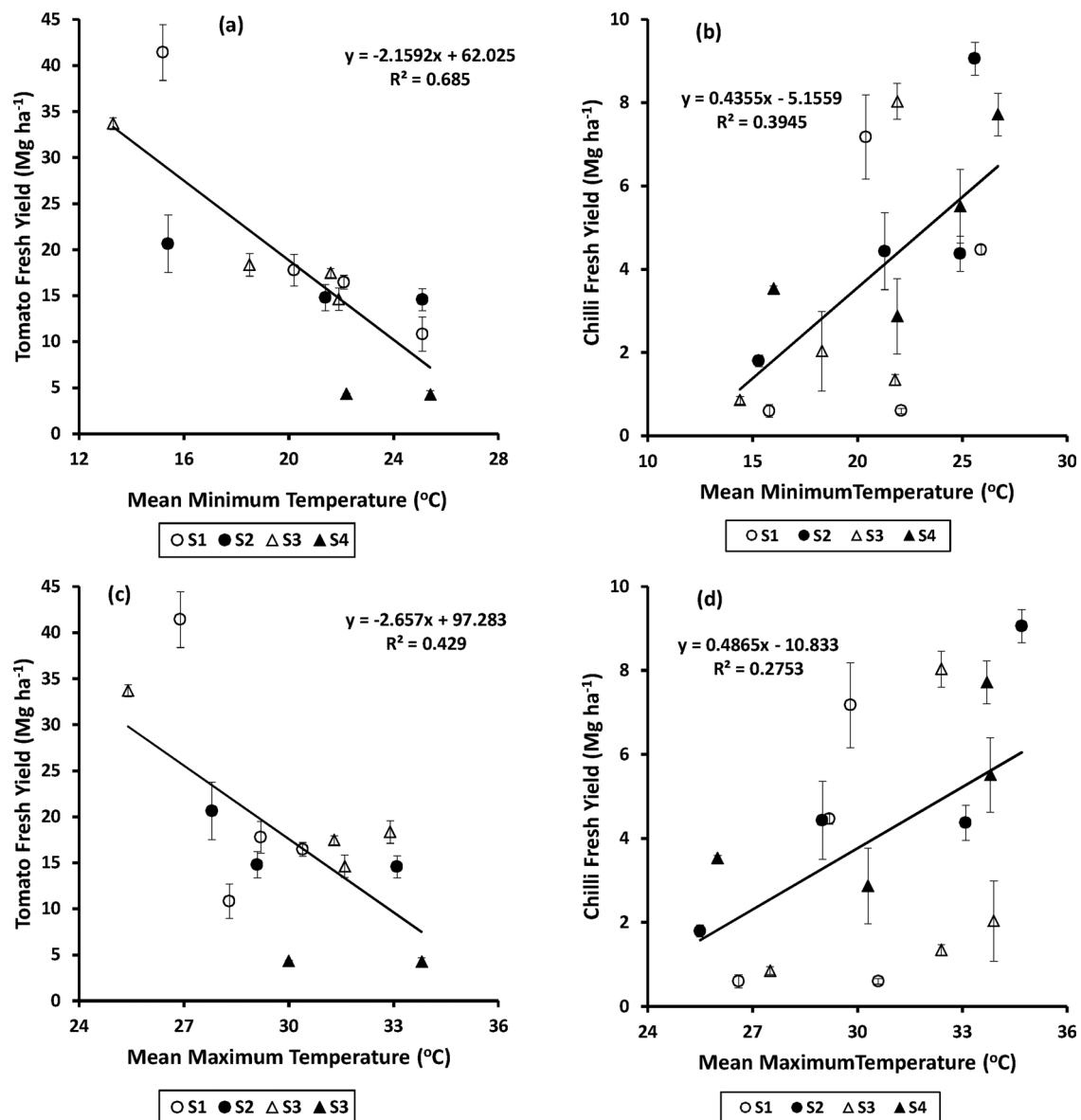


Fig. 3. Variation of fresh fruit/pod yields of tomato (a and c) and chilli (b and d), with seasonal mean minimum and maximum air temperatures, respectively. S1–S4 denote the four cropping seasons. Each data point is a mean of three replicate plots. Vertical error bars indicate the standard error of mean.

4.2. Parameters of yield determination during the responses to temperature

The absence of significant correlations between the two major yield components (i.e. fruit/pod number per plant and individual fruit/pod weight) in both crops showed that they are independently determined during the crops' responses to increasing temperature. However, different yield components exerted controlling influences in determining the yields of the two crops. Whereas variation in the number of fruits per plant (NPP) had a controlling influence on the yield response of chilli, variation in the individual fruit weight (IFFW) controlled the yield response of tomato. The positive temperature response of NPP of chilli show that its reproductive processes (i.e. flower initiation and development, fertilization and pod development) are less-sensitive to increasing temperatures, thus making it more suitable to be included in cropping systems in a future warmer climate. In contrast, the negative temperature response of IPFW of tomato shows that biomass partitioning to initiated fruits decreases with increasing temperature.

4.3. Experimental approach used in the present work

The present work has used an experimental approach under actual field conditions to estimate the impacts of increasing temperature on tomato and chilli. A primary assumption in the multi-locational experimental design used here is that temperature variation across the four experimental locations is the principal environmental factor controlling the growth and yield formation of crops. Results of multiple regression analysis (Supplementary Tables S11 and S12) confirmed the validity of our initial assumption. Parallel instances of such natural environmental gradients being used to determine plant response to a given environmental factor could be found in the substantial number of studies that have used altitudinal gradients (Körner, 2007). These have examined the impacts of variations in air temperature and/or partial pressure of CO₂ on a wide range of plant processes (Woodward, 1986; Caldera et al., 2017). In the present work, there were a few occurrences of extreme weather events which either slowed down or destroyed the crops. Severe drought prevented the tomato crops from completing their life cycle during Seasons 2 and 4 at Kilinochchi and Season 4 at Rahangala while excessive mid-seasonal rainfall delayed flowering of

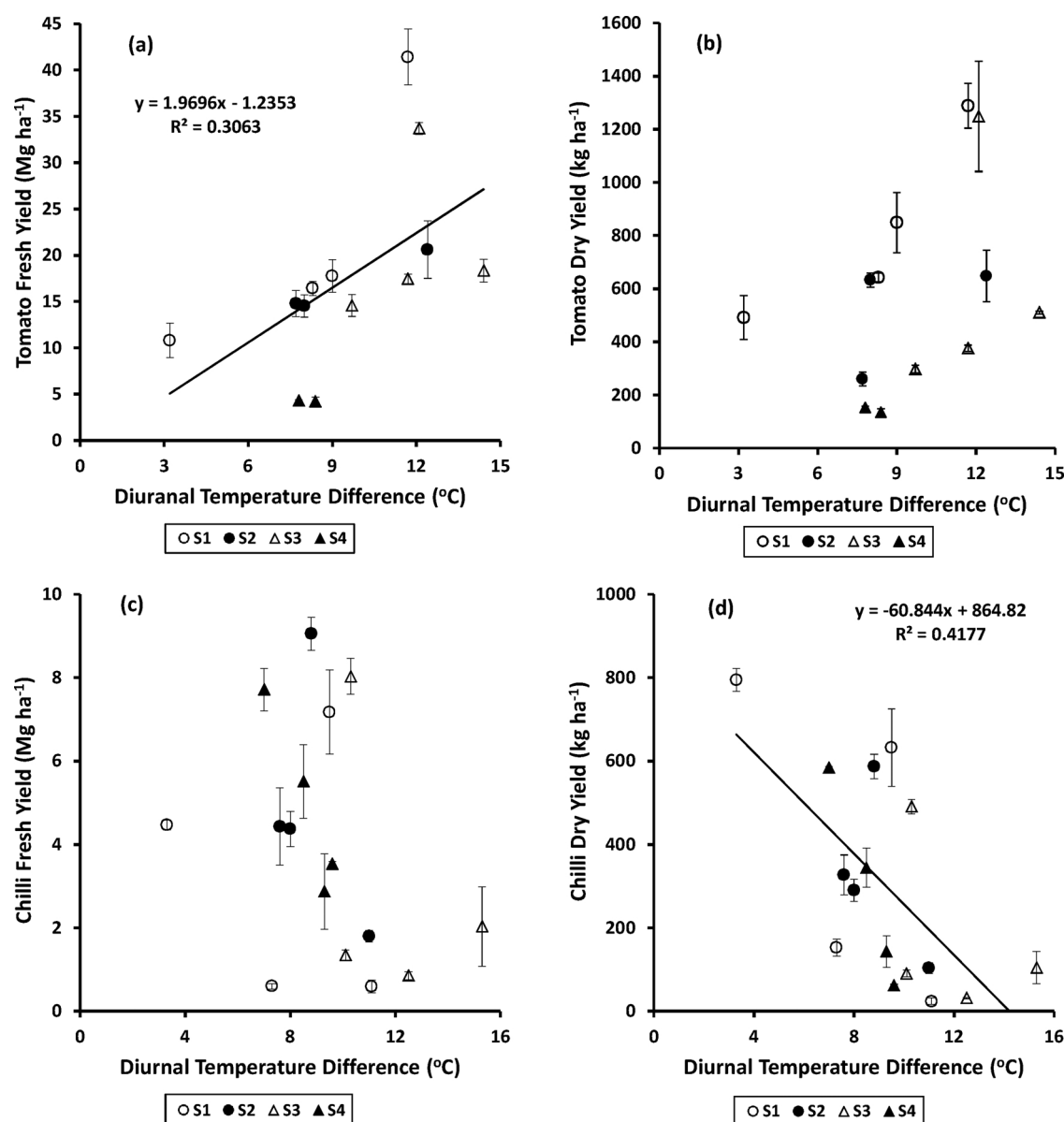


Fig. 4. Variation of fresh and dry fruit yields (a and b) of tomato and fresh and dry pod yields (c and d) of chilli with seasonal mean diurnal temperature difference. S1–S4 denote the four cropping seasons. Each data point is a mean of three replicate plots. Vertical error bars indicate the standard error of mean.

both tomato and chilli at Maha-illuppallama during Season 1. Apart from the above events, crop management in all locations ensured that crops grew without any limitations of water and nutrients through irrigation and fertilizer application respectively according to specified recommendations. Management of pests, diseases and weeds by adopting recommended preventive and control measures ensured that crop yields were not limited by biotic stress factors. These ensured that variation in temperature across the altitudinal gradient was the principal driver of the observed variations in crop growth and yield. A similar approach has been used to assess the impacts of increasing temperature on growth and yield of other crops such as potato (Abhayapala et al., 2015), mung bean (Malaviarachchi et al., 2016) and maize (Malaviarachchi et al., 2015). This approach, where temperature, rather than precipitation, is considered as the principal determinant of crop yields is supported by findings of Lobell and Field (2007), Lobell and Burke (2008), Li et al. (2010) and Porter et al. (2014), which demonstrate the greater influence of temperature variation, as opposed to that of rainfall variation, in determining crop yields across a broad spatial scale.

Incidence of virus diseases was observed in both crops. In a parallel study on the same experimental crops (Prasannath et al., 2015), the virus disease incidence in tomato showed a significant ($P < 0.01$), but weak ($R^2 = 0.22$) positive linear relationship with seasonal mean temperature (T_a). However, this is unlikely to have had a significant influence on yields as virus disease incidence in tomato and chilli did not exceed 5% in any of the locations. Virus disease incidence of both crops did not show significant relationships with the variation in rainfall and RH across the locations. Therefore, it is unlikely that observed variations in the incidence of virus diseases could have had a controlling influence on the differential temperature responses of tomato and chilli.

There is still considerable debate on the merits and limitations of different methods employed for assessing the impacts of climate change on crop yields (Ainsworth et al., 2008; Porter et al., 2014). The present approach complements the single-location impact assessments using FACE or open top chambers (OTCs) where only two environments (i.e. current and future) are used as experimental treatments in comparison to the several environments used in the present approach. As such, the

present work has established temperature response functions across a wider temperature range than those used in FACE or OTC work. As the crops have been grown under open field conditions over larger plots without the presence of chambers or methods of CO₂ and/or temperature elevation, the observed growth and yield responses are more representative of actual farming conditions. Furthermore, the temperature response functions obtained in the present work can be used to validate predictions from process-based simulation models for assessing climate change impacts on crops and thereby complements the simulation modeling approach as well (Craufurd et al., 2013).

4.4. Estimated cardinal temperatures of tomato and chilli and their relevance to yield determination

In the present study, the cardinal temperatures of both crops were estimated based on their rate of progress to maturity. For tomato, the estimated T_{opt} of 23.6 °C is within range of 20–26 °C that has been reported in literature (De Koning, 1994; Adams et al., 2001; Van der Ploeg and Heuvelink, 2005). However, the estimated T_b and T_{ce} of 11.8 and 35.4 °C in the present work are higher than the respective ranges of 5–7 °C (Adams et al., 2001; Hatfield et al., 2009) and 30–32 °C (Hatfield et al., 2009). It is possible that these differences are due to genotypic variation as the cultivar used in the present work is adapted to warmer tropical climates than to cooler temperate and sub-tropical climates where most of the reported work has been carried out. It is highly likely that adaptation to warmer temperatures would have pushed both the base and ceiling temperatures towards higher values.

In contrast to tomato, there is only limited published literature on the cardinal temperatures and the temperature response functions of chilli. The estimated T_{opt} 24.6 °C in the present work, which is based on the rate of progress to maturity, is within the optimum range of 20–25 °C for growth and yield as reported by Saha et al. (2010). The estimated T_b of 13.9 °C is within the reported range of 12–15 °C for the minimum temperature for growth and yield (Anonymous, 2013a, 2013b, 2015). However, the estimated T_{ce} is higher than the reported range of 30–32 °C (Anonymous, 2013a, 2013b, 2015), but is still below the T_{ce} of 40.4–41.8 °C for pollen germination and pollen tube growth of *Capsicum* species (Reddy and Kakani, 2007). However, in agreement with the above temperature thresholds, growth and yield of chilli in the present work increased across the whole range of seasonal mean temperatures experienced (i.e. 19.6–30.0 °C).

5. Conclusion

The present work demonstrates the feasibility of increasing resilience of smallholder tropical farming systems to climate change by appropriate selection of crops such as chilli which show a positive yield response to increasing future temperatures in place of temperature-sensitive crops such as tomato. The demonstration of contrasting responses of different crops to increasing temperature also highlights the possibility of similar situations with regard to other crops which form the wide range of diverse crop species in tropical smallholder farms. Our work also shows that different yield components and physiological relationships dominate and determine the yield responses of different crops to increasing temperature. Based on these results, it is concluded that replacement of high temperature-sensitive crops such as tomato in tropical smallholder cropping systems with crops such as chilli, which increases its productivity at higher temperatures, could constitute an important adaptation option to minimize the adverse impacts of long-term climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2017.10.027>.

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